

Efficiency of Indirect Selection for Dry Matter Yield Based on Fresh Matter Yield in Perennial Ryegrass Sward Plots

Patrick Conaghan,* Michael D. Casler, Pádraig O'Kiely, and Leslie J. Dowley

ABSTRACT

Forage dry matter yield (DMY) is a high-priority trait in breeding perennial ryegrass (*Lolium perenne* L.). However, determining dry matter concentration is highly labor intensive. For a similar level of resources, indirect selection based on fresh matter yield (FMY) would allow a greater number of replicates, genotypes, or both to be evaluated. Our objective was to estimate the efficiency of indirect selection for DMY based on FMY of pure perennial ryegrass sward plots. Over a 14-yr period, replicated trials, containing perennial ryegrass genotypes of similar ploidy and maturity category, were sown in Ireland and assessed for DMY and FMY at each harvest over two consecutive years. Forage was generally surface dry when harvested. The estimated efficiency of indirect selection based on two replicates and comparable selection intensity was high (≥ 0.80). Simulation models indicated that resources would be used more efficiently by evaluating more genotypes than by increasing the number of replicates. For example, doubling the number of plots to increase the number of replicates from two to four indicated an increase in the efficiency of indirect selection from a mean 0.88 to 0.94. However, doubling the number of plots and including more genotypes, facilitating greater selection intensity, indicated an increase in the efficiency of indirect selection from a mean 0.88 to 1.04. This study indicates that FMY can be used successfully as an indirect selection method of increasing DMY in perennial ryegrass swards.

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Abbreviations: DM, dry matter; DMY, dry matter yield; FMY, fresh matter yield.

PERENNIAL RYEGRASS (*Lolium perenne* L.) is arguably the most widely sown perennial forage grass in temperate regions and the key component of the most productive swards (Wilkins, 1991). While significant improvements in productivity have been achieved through breeding, the potential for further improvement is considerable. Forage grass breeding is at a very early stage, and most of the useful genetic variation within and between forage grass species has yet to be utilized (Wilkins and Humphreys, 2003).

Yield has primary importance as a breeding objective since land is valuable and there must be an adequate return on the capital invested (Wilkins, 1991). Increased grass production may facilitate (i) an increase in the stocking rate, (ii) a reduction in the dependence on alternative feeds, (iii) a reduction in the need to buy fodder or rent additional grassland, and (iv) the release of land for alternative enterprises such as cereals. The seasonal pattern of production may be as important as annual production. For most livestock enterprises, both the availability of grass and the demand for it are continuously fluctuating, with the result that its economic value over the season will change (Doyle and Elliott, 1983).

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Assessing genetic differences in forage grass production is not straightforward. While most grass breeding takes place on an individual plant basis, there is often poor agreement between individual spaced plants and sward plots in yield (Casler et al., 1996). The considerable degree of genetic independence between yield of reproductive growth and yield of vegetative growth can lead to genotype \times harvest-frequency interactions for annual yield, necessitating genotype evaluation under both conservation (infrequent cutting) and frequent-cutting managements (Wilkins and Humphreys, 2003). Genotype \times year interactions for yield require that evaluations of perennial forage grasses are typically conducted for 3 yr, although data are not usually collected during the establishment year.

Estimation of yields on a dry matter (DM) basis is necessary for meaningful comparisons among experiments and feeds because of the variable content of both internal and external water in fresh samples. Besides genetics, factors influencing dry matter yield (DMY) include soil condition, climate and weather, season and, management. Consequently DMY is highly variable across time.

The relationship between DMY and fresh matter yield (FMY) is a function of forage DM concentration. Ploidy, stage of maturity, and soil nutrient supply all influence internal water content, whereas the external water content is exceedingly variable, influenced by both prevailing weather conditions and the yield, morphology, and growth habit of the crop (Knight et al., 1996). In a single trial of 15 genotypes, Frandsen (1986) recorded a highly significant and positive simple correlation between DMY and FMY in perennial ryegrass sward plots. Furthermore, broad sense heritability was greater for FMY than DMY. If the selection intensity (i) for both traits is the same, indirect selection will be of greater or similar efficiency than direct selection if

$$r_G h_y \geq h_x \quad [1]$$

where r_G is the genetic correlation between traits, and h_y and h_x are the square roots of the heritabilities of the secondary and primary traits, respectively (Gallais, 1984). Hence, the findings of Frandsen (1986), albeit on a limited scale, suggest significant potential for indirect selection for DMY using FMY as the selection criterion.

Resources are always limited in plant breeding programs, restricting the number of plots or plants that can be evaluated. Indirect selection for DMY on FMY, provided it eliminated the requirement to sample and dry forage, would allow a greater number of plots to be evaluated for a given level of resources. The extra plots could be used to (i) increase the number of replicates, improving the precision and accuracy of measurements, (ii) test a greater number of genotypes, facilitating a greater i while still selecting a fixed number of genotypes, or (iii) both. All

three options may counteract any potential genetic inefficiency in indirect selection and, in addition, allow greater gain to be made on other traits selected on a plot level.

The objective of this study was to estimate the efficiency of indirect selection for DMY based on FMY measured on perennial ryegrass sward plots.

MATERIALS AND METHODS

Germplasm and Management

Between 1992 and 2004, 283 perennial ryegrass trials were sown at the Oak Park Research Centre, Carlow, Ireland (52°5' N, 6°55' W and 58 m above sea level) on a free-draining gray brown umbrisol soil. The experimental design of each trial was a randomized complete block with two replicates. Trials contained cultivars plus families, experimental synthetics, or both (hereafter collectively called *genotypes*). Genotypes of different ploidy and typically maturity category (i.e., early, intermediate or late) were arranged in separate trials. Plots (6 \times 1.5 m) were sown as pure swards, following full cultivation, at 30 kg ha⁻¹ for diploids or 35 kg ha⁻¹ for tetraploids. Extra plots were sown at the ends of each row to reduce border effects.

During the establishment year, plots were sprayed with a herbicide mixture for control of perennial and annual broad-leaved weeds and cut at 4- to 6-wk intervals, but no measurements were taken. Plots were limed and fertilized according to soil-test recommendations. For 2 consecutive years thereafter, trials were subjected to either a conservation management program involving four harvests per year ($n = 146$ trials, mean 19.7 ± 0.4 genotypes trial⁻¹) or a frequent-cutting management program involving seven to nine harvests per year ($n = 137$ trials, mean 19.3 ± 0.1 genotypes trial⁻¹). Fresh matter yield was determined by harvesting the entire plot to a stubble height of 5 cm above ground level using a plot harvester (Haldrup, Lögstör, Denmark). Harvest dates were modified according to prevailing weather conditions so that ideally, forage was harvested without excess external water. Dry matter determinations were made on randomly taken forage samples of each plot by drying in a forced air circulation oven at 90° C for 30 h and were used to adjust plot FMY to a DM basis. Plot yields from multiple harvests within a year were summed to give annual and the combined first and second harvest yields under the conservation management program, and annual, early spring, mid-late spring, early-midsummer and, late summer-autumn yields under the frequent-cutting management program. Fertilizer was applied to the conservation management trials at a rate of 120 kg N, 13 kg P, and 50 kg K ha⁻¹ mid-March, and a further 75 kg N, 8 kg P, and 31 kg K ha⁻¹ immediately after harvests 1, 2, and 3. Fertilizer was applied to the frequent-cutting management trials at a rate of 75 kg N, 8 kg P, and 31 kg K ha⁻¹ mid-February, with a further 40 kg N, 4 kg P, and 17 kg K ha⁻¹ applied immediately after all but the final harvest each year.

Statistical Analyses

Results were analyzed using the SAS statistical package (SAS Institute, Cary, NC). For each trial, analyses of variance and covariance between DMY and FMY were conducted using the model

$$Y_{ijk} = \mu + B_j + Y_k + BY_{jk} + G_i + BG_{ij} + YG_{ik} + \varepsilon_{ijk} \quad [2]$$

where Y_{ijk} is the observation made on the i th genotype of the j th block in the k th year, μ is the overall mean, B_j is the j th block effect, Y_k is the k th year effect, BY_{jk} is the interaction effect of the j th block with the k th year, G_i is the i th genotype effect, BG_{ij} is the interaction effect of the i th genotype with the j th block, YG_{ik} is the interaction effect of the i th genotype with the k th year, and ε_{ijk} is the residual of the ijk th plot in the k th year. All effects were assumed to be random. Year was assumed to be random because differences between years were primarily due to weather variation. Genotypes were assumed to be random because inferences were applied to the population from which they were drawn. Variance and covariance components were estimated by equating mean squares and mean products to their expectations (Gaylor et al., 1970). Broad sense heritability (H) was estimated as

$$H = \frac{\sigma_G^2}{\sigma_G^2 + \frac{\sigma_{GB}^2}{b} + \frac{\sigma_{GY}^2}{y} + \frac{\sigma_\varepsilon^2}{by}} \quad [3]$$

where σ_G^2 , σ_{GB}^2 , σ_{GY}^2 , σ_ε^2 , b , and y are the genotype, genotype \times block, genotype \times year, and within-trial error variances, and the number of blocks and years of testing, respectively. If the genotype F -test for DMV was not significant at $P < 0.25$, or the H for either DMV or FMV was negative, data from that trial were discarded from all analyses and calculations. The r_G between DMV and FMV was calculated as

$$r_G = \frac{\text{COV}_{\text{DF}}}{\sqrt{\sigma_{\text{GD}}^2 \sigma_{\text{GF}}^2}} \quad [4]$$

where COV_{DF} is the genetic covariance between DMV and FMV, and σ_{GD}^2 and σ_{GF}^2 are the genotypic variances for DMV and FMV, respectively.

The relative selection efficiency of indirect selection for DMV on FMV relative to direct selection was determined as

$$\text{CR}_D / \text{R}_D = \frac{k_F r_G h_F}{k_D h_D} \quad [5]$$

where k_F and k_D are the standardized selection differential imposed for FMV and DMV, respectively, and h_F and h_D represent the square root of the broad sense heritabilities for FMV and DMV, respectively (Falconer and Mackay, 1996). The effect of increasing the number of replicates (blocks) for determining FMV from 2 to 10 on the efficiency of indirect selection versus direct selection on two blocks of DMV was investigated hypothetically by varying the number of blocks in the calculation of h_F in Eq. [3] and [5]. The effect of increasing selection intensity for FMV from 10 to 2% on the efficiency of indirect selection relative to direct selection with selection intensity for DMV held constant at 10% was investigated hypothetically by modifying k_F in Eq. [5].

For each harvest period, DMV based on means over two blocks was considered the best available measure of DMV. This was compared relative to DMV based on one block (Block 1 and Block 2), FMV based on one block (Block 1 and Block 2) and means over two blocks, and a combination of one block each of DMV and FMV (Block 1 DMV + Block 2 FMV and Block 2

DMV + Block 1 FMV) by Spearman's rank correlation coefficients. The combined yield of one block each of DMV and FMV was computed on a DM basis by adjusting the FMV of each genotype by either its corresponding DM concentration in the other block or the mean DM concentration of all genotypes in the other block. The five genotypes with the highest DMV based on DMV means over two blocks were defined as the "correct selections." A counting was made on the number of correct selections in the top five ranked genotypes based on DMV from one block (Block 1 and Block 2), FMV from one block (Block 1 and Block 2) and means over two blocks, and a combination of one block each of DMV and FMV (Block 1 DMV + Block 2 FMV and Block 2 DMV + Block 1 FMV) as calculated above.

The above statistics were calculated on an individual trial basis. Standard errors were computed from the variance among all trials.

RESULTS AND DISCUSSION

Between 15 and 43% of trials, depending on harvest period, showed no evidence of differences ($P < 0.25$) among genotypes for DMV, or indicated negative H estimates for either DMV or FMV, and were discarded from the analysis (Table 1). The rate of increase in genetic potential for forage DMV in perennial ryegrass has been estimated as 0.25 to 0.6% per annum (Wilkins and Humphreys, 2003), demonstrating that differences in yield between established cultivars and elite germplasm are likely to be small and difficult to detect at stringent significant levels ($P < 0.05$) (Smith and Kearney, 2002). However, Casler and Undersander (2000) recommended that trials should not be discarded solely on the basis of low statistical precision. Therefore, $P < 0.25$ for genotypes was chosen as a less-conservative critical value for rejecting trials from the analysis.

Yields of DM were relatively high and comparable to those of Gilliland (2006) for similarly managed conservation and frequent-cutting trials (Table 1). Mean DM concentration was relatively high for leafy forage (Table 1) (Bailey,

Table 1. Number of trials (n) included in analyses,[†] and their mean \pm SE dry and fresh matter yields (DMV and FMV), and dry matter concentration.

Period	<i>n</i>	DMY	FMY	Dry matter
		—— t ha ⁻¹ ——		%
Conservation management				
First cut	118	6.84 ± 0.08	38.10 ± 0.46	18.2 ± 0.1
Second cut	83	4.42 ± 0.08	21.59 ± 0.45	20.9 ± 0.3
First + second cut	111	11.38 ± 0.12	60.68 ± 0.77	19.4 ± 0.2
Annual	102	17.41 ± 0.17	89.57 ± 1.05	20.2 ± 0.1
Frequent-cutting management				
Early spring	117	2.22 ± 0.06	11.05 ± 0.33	20.2 ± 0.2
Mid-late spring	100	4.13 ± 0.08	23.39 ± 0.45	17.7 ± 0.1
Early-mid summer	87	3.86 ± 0.06	17.70 ± 0.32	22.3 ± 0.2
Late summer-autumn	108	4.12 ± 0.09	19.62 ± 0.43	21.0 ± 0.1
Annual	104	14.40 ± 0.13	72.11 ± 0.81	20.4 ± 0.1

[†]Genotype F -test for DMV < 0.25 and, positive heritability for DMV and FMV.

1973). Samples were typically at the upper end or above the threshold of 16 to 18% DM concentration, indicative of grass free from external water (O'Donovan and Dillon, 1999), confirming that the objective to harvest plots when forage was surface dry was largely successful.

Both traits had smaller variances for genotype \times block and genotype \times year interactions than genotype effects, indicating that genotype performance was relatively consistent across blocks and years (Table 2). In this context, genotype \times year effect is principally a consequence of age-of-stand effects, year-to-year meteorological changes, and their effect on soil conditions and disease incidence. These findings are supported by those of Talbot (1984) with similarly managed perennial ryegrass trials in the United Kingdom. The relative magnitudes of genotype to error variance for each harvest period were generally greater for FMY compared with DMY, particularly for the conservation management trials (Table 2). In the determination of FMY, only one measurement was taken: plot weight. Two further measurements, sample fresh and dry weight, each contributing to error, were needed to correct FMY to DMY. Because experimental errors from different sources are additive, the relatively lower error variances for FMY, relative to DMY, may be due to the simplicity of a trait determined by a single measurement. However, the relative magnitudes of genotype to genotype \times block and genotype \times year variance for each harvest period were typically greater for FMY than DMY. Consequently, esti-

mates of H were similar for both traits at corresponding harvest periods (Table 3), in contrast to Frandsen (1986), who reported slightly higher H for FMY. Overall estimates of H were relatively high although values of 0.63 to 0.92 have been previously reported for annual DMY under conservation and frequent-cutting managements (Rhodes, 1971; Devey et al., 1989).

There was a high, positive r_G between traits for all harvest periods (Table 3), indicating that FMY provided a reliable assessment of DMY. Previous studies have reported phenotypic correlations of 0.96 and 0.97 between DMY and FMY in perennial ryegrass and *Lolium multiflorum* Lam. spaced plants, respectively (Frandsen and Fritsen, 1982; Mittelman et al., 2006). Frandsen (1986) did not present the data for the correlations between DMY and FMY in perennial ryegrass sward plots but described them as highly significant and positive. Phenotypic correlations between traits in the current study ranged between 0.78 and 0.96, depending on harvest period. Factors affecting DM concentration among genotypes, and by extension r_G , include yield, leaf-to-stem ratio, or both, as management and ploidy were constant within trials. Higher-yielding genotypes may have lower DM concentrations because of lower drying rates in the standing crop, while increasing the proportion of mature stem tissue tends to increase DM concentration of total forage (Bailey, 1973). Even within maturity category, significant differences among genotypes in the proportion of leaf to stem have been found (Gilliland et al., 2002).

Low overall yields for a particular harvest period favors a high r_G as relative differences among genotypes in their external water content would be diminished owing to increased drying rates. The effect of leaf-to-stem ratio depends on the stage of reproductive development at harvest. Early spring growth and, to a lesser degree, late summer–autumn growth are predominately vegetative, producing swards of high leaf content irrespective of genotype (Gilliland et al., 2002). The negligible differences among genotypes in the proportion of leaf to stem in early spring and late summer–autumn under a frequent-cutting management would favor a high r_G for these periods. The positive effects of low yield and high estimated leaf content on r_G are evident for early spring yield, which was found to have the highest r_G of all harvest periods.

The efficiency of indirect selection for DMY based on FMY measured over two blocks ranged between 0.80 and 1.00 (Table 3). There are few, if any, instances wherein indirect selection with one secondary trait is clearly superior to direct selection for DMY

Table 2. Variance component estimates[†] \pm SE for dry and fresh matter yields (DMY and FMY) from two-block conservation and frequent-cutting management trials.

Trait	Period	σ^2_G	σ^2_{GB}	σ^2_{GY}	σ^2_ϵ
Conservation management					
DMY	First cut	0.23 \pm 0.013	0.03 \pm 0.008	0.04 \pm 0.007	0.26 \pm 0.019
	Second cut	0.07 \pm 0.006	0.00 \pm 0.004	0.03 \pm 0.006	0.12 \pm 0.013
	First + second cut	0.30 \pm 0.017	0.07 \pm 0.016	0.07 \pm 0.010	0.38 \pm 0.024
	Annual	0.52 \pm 0.031	0.17 \pm 0.031	0.15 \pm 0.019	0.52 \pm 0.028
FMY	First cut	7.34 \pm 0.447	1.33 \pm 0.211	2.08 \pm 0.190	3.74 \pm 0.366
	Second cut	1.63 \pm 0.137	0.48 \pm 0.116	0.96 \pm 0.085	1.43 \pm 0.138
	First + second cut	9.14 \pm 0.511	3.76 \pm 0.428	3.58 \pm 0.241	4.88 \pm 0.393
	Annual	15.13 \pm 0.9231	8.10 \pm 1.098	5.76 \pm 0.468	7.39 \pm 0.533
Frequent-cutting management					
DMY	Early spring	0.05 \pm 0.004	0.01 \pm 0.001	0.02 \pm 0.002	0.03 \pm 0.003
	Mid–late spring	0.03 \pm 0.002	0.00 \pm 0.001	0.01 \pm 0.002	0.03 \pm 0.003
	Early–midsummer	0.04 \pm 0.002	0.01 \pm 0.002	0.02 \pm 0.002	0.03 \pm 0.002
	Late summer–autumn	0.04 \pm 0.003	0.03 \pm 0.003	0.02 \pm 0.002	0.04 \pm 0.003
	Annual	0.26 \pm 0.015	0.16 \pm 0.017	0.08 \pm 0.008	0.15 \pm 0.010
FMY	Early spring	1.82 \pm 0.164	0.22 \pm 0.053	0.54 \pm 0.049	0.97 \pm 0.077
	Mid–late spring	1.21 \pm 0.084	0.20 \pm 0.049	0.63 \pm 0.064	0.95 \pm 0.110
	Early–midsummer	0.91 \pm 0.060	0.41 \pm 0.060	0.48 \pm 0.039	0.74 \pm 0.057
	Late summer–autumn	1.17 \pm 0.078	0.79 \pm 0.102	0.56 \pm 0.053	1.05 \pm 0.087
	Annual	8.49 \pm 0.472	5.85 \pm 0.566	3.20 \pm 0.291	4.62 \pm 0.443

[†] σ^2_G , σ^2_{GB} , σ^2_{GY} , and σ^2_ϵ indicate genotype, genotype \times block, genotype \times year, and error variances, respectively.

(Gallais, 1984). Indirect selection is performed not necessarily because it is more effective than direct selection but because a secondary trait is easier, quicker, or cheaper to evaluate than the primary trait (Bernardo, 2002). The savings in costs (e.g., money, labor, time) achieved by not sampling and drying forage in the measurement of FMY could be reallocated to the evaluation of more plots, thereby increasing the number of replicates, genotypes, or both. Increasing the number of genotypes evaluated is the only way to increase i while maintaining a fixed number of individuals or families that are recombined to form the next cycle. Increasing i without increasing the number of genotypes evaluated would result in recombining a smaller number of individuals or families and possibly inbreeding depression (Falconer and Mackay, 1996). The benefit of increasing replication or i on the efficiency of indirect selection followed a curvilinear pattern (Fig. 1) similar to that observed by England (1977). The benefit:cost ratio was significantly greater based on increasing i rather than that based on increasing the number of replicates. For example, doubling the number of plots to increase the number of replicates from two to four increased the efficiency of indirect selection from a mean 0.88 to 0.94. However, doubling

Table 3. Broad sense heritability estimates for dry and fresh matter yields (DMY and FMY), genetic correlations (r_g) between DMY and FMY and the relative efficiency of indirect selection for DMY based on FMY relative to direct selection (CR_D/R_D) from two-block conservation and frequent-cutting management trials.

Period	<u>Broad sense heritability</u>		r_G	CR_D/R_D
	DMY	FMY		
Conservation management				
First cut	0.68 ± 0.013	0.70 ± 0.017	0.94 ± 0.021	0.95 ± 0.022
Second cut	0.63 ± 0.019	0.56 ± 0.023	0.98 ± 0.029	0.90 ± 0.025
First + second cut	0.64 ± 0.014	0.63 ± 0.015	0.85 ± 0.026	0.83 ± 0.022
Annual	0.63 ± 0.015	0.61 ± 0.017	0.84 ± 0.019	0.83 ± 0.023
Frequent-cutting management				
Early spring	0.67 ± 0.015	0.69 ± 0.015	0.98 ± 0.004	1.00 ± 0.009
Mid-late spring	0.65 ± 0.017	0.63 ± 0.018	0.87 ± 0.013	0.85 ± 0.019
Early-midsummer	0.61 ± 0.014	0.57 ± 0.020	0.92 ± 0.015	0.87 ± 0.018
Late summer-autumn	0.59 ± 0.014	0.57 ± 0.015	0.92 ± 0.010	0.89 ± 0.012
Annual	0.62 ± 0.015	0.60 ± 0.020	0.84 ± 0.031	0.80 ± 0.018

the number of plots and including more genotypes, increasing i from 10 to 5% while still selecting the same number of genotypes, increased the efficiency of indirect selection from a mean 0.88 to 1.04. Previous studies also indicate that resources would be used more efficiently by evaluating more genotypes than by introducing excessive replication (Brown and Glaz, 2001; Osorio et al., 2003).

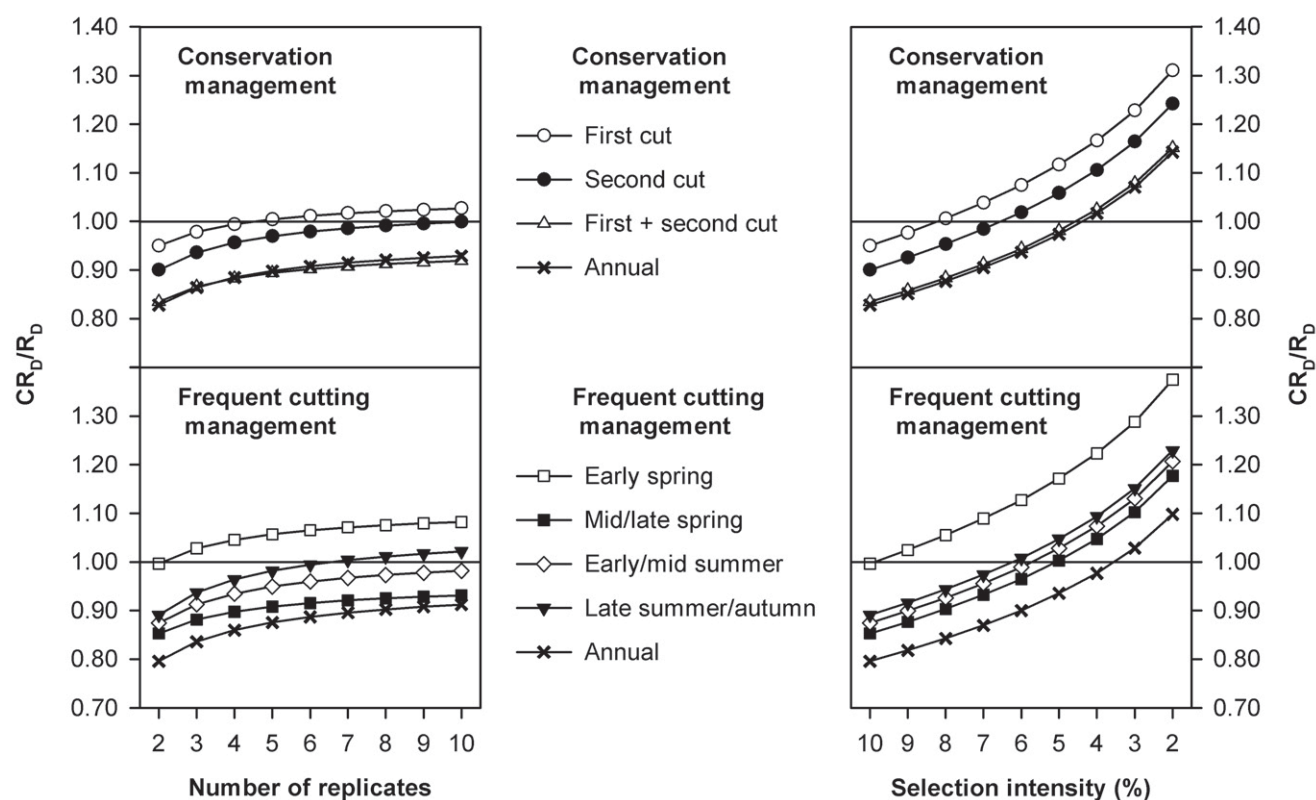


Figure 1. Effect of varying the number of replicates for determining fresh matter yield (FMY) or the selection intensity (i) for FMY on the efficiency of indirect selection for dry matter yield (DMY) versus direct selection (CR_D/R_D) on two replicates of DMY at a constant i of 10% in conservation and frequent-cutting management trials. Assuming a fixed number of genotypes are selected at each i , four replicates or i of 5%, and 10 replicates or i of 2% correspond to a double and fivefold increase in plot numbers, respectively, relative to trials of two replicates and i of 10%.

Table 4. Spearman's rank correlation coefficients between dry matter yield (DMY) based on means over two blocks with DMY from one block, fresh matter yield (FMY) from one block and means over two blocks, and a combination of one block each of DMY and FMY with FMY of each genotype adjusted to a dry matter (DM) basis by either its corresponding DM concentration in the other block (by entry) or the mean DM concentration of all genotypes in the other block (by trial).

Period	DMY	FMY		DMY/FMY	
	1 block	1 block	2 blocks	By entry	By trial
Conservation management					
First cut	0.86 ± 0.005	0.74 ± 0.008	0.80 ± 0.010	0.91 ± 0.004	0.89 ± 0.005
Second cut	0.87 ± 0.006	0.71 ± 0.011	0.80 ± 0.013	0.90 ± 0.005	0.89 ± 0.005
First + second cut	0.85 ± 0.005	0.67 ± 0.010	0.74 ± 0.013	0.89 ± 0.005	0.88 ± 0.005
Annual	0.85 ± 0.005	0.69 ± 0.010	0.77 ± 0.012	0.90 ± 0.004	0.90 ± 0.004
Frequent-cutting management					
Early spring	0.89 ± 0.004	0.86 ± 0.005	0.94 ± 0.004	0.97 ± 0.001	0.97 ± 0.001
Mid-late spring	0.89 ± 0.005	0.75 ± 0.008	0.82 ± 0.010	0.92 ± 0.003	0.93 ± 0.003
Early-mid summer	0.88 ± 0.005	0.77 ± 0.009	0.86 ± 0.010	0.94 ± 0.003	0.95 ± 0.003
Late summer-autumn	0.86 ± 0.005	0.77 ± 0.007	0.89 ± 0.007	0.95 ± 0.002	0.96 ± 0.002
Annual	0.86 ± 0.006	0.72 ± 0.009	0.82 ± 0.010	0.93 ± 0.003	0.96 ± 0.002

The value of the loss in DMY gains with indirect selection will depend on the harvest period, as the economic value of extra grass production can vary enormously through the growing season. Where the increase in grass output is mainly confined to one period, and that period is one in which grass supply already exceeds demand, the extra grass production may have no value (Doyle and Elliott, 1983). In this regard, although annual production is commonly presented as an index of cultivar performance, it is in practice of limited value. Under grazing in cool temperate maritime regions, animal demand often exceeds grass supply during the early spring and late summer-autumn period with a significant surplus in supply during the intervening period. First cut accounts for over 70% of the silage harvested in Ireland, with second

Table 5. Mean ± SE numbers of "correct" selections (five possible) from harvests based on dry matter yield (DMY) from one block, fresh matter yield (FMY) from one block and means over two blocks, and a combination of one block each of DMY and FMY with FMY of each genotype adjusted to a dry matter (DM) basis by either its corresponding DM concentration in the other block (by entry) or the mean DM concentration of all genotypes in the other block (by trial).

Period	DMY	FMY		DMY/FMY	
	1 block	1 block	2 blocks	By entry	By trial
Conservation management					
First cut	3.8 ± 0.05	3.3 ± 0.06	3.5 ± 0.08	4.0 ± 0.05	4.0 ± 0.05
Second cut	3.8 ± 0.06	3.1 ± 0.07	3.4 ± 0.09	3.9 ± 0.06	3.9 ± 0.06
First + second cut	3.8 ± 0.05	3.1 ± 0.06	3.3 ± 0.08	3.9 ± 0.05	3.9 ± 0.05
Annual	3.8 ± 0.05	3.0 ± 0.06	3.3 ± 0.08	4.0 ± 0.05	4.0 ± 0.05
Frequent-cutting management					
Early spring	4.0 ± 0.05	3.8 ± 0.05	4.2 ± 0.06	4.5 ± 0.04	4.5 ± 0.04
Mid-late spring	3.8 ± 0.06	3.2 ± 0.06	3.3 ± 0.09	4.0 ± 0.05	4.1 ± 0.05
Early-mid summer	3.8 ± 0.06	3.3 ± 0.07	3.7 ± 0.08	4.2 ± 0.05	4.3 ± 0.05
Late summer-autumn	3.8 ± 0.05	3.4 ± 0.06	3.9 ± 0.08	4.3 ± 0.04	4.4 ± 0.04
Annual	3.8 ± 0.06	3.2 ± 0.06	3.6 ± 0.08	4.1 ± 0.05	4.3 ± 0.05

harvests from the same area accounting for most of the remainder (Drennan et al., 2005). If the primary goal is to increase DMY of early spring, late summer-autumn and first-cut silage, indirect selection based on FMY is highly effective, offering a mean 0.95 the gain of direct selection at a comparable *i*. If the number of genotypes evaluated is doubled and *i* for FMY increased from 10 to 5%, indirect selection is more effective than direct selection at *i* of 10% with a mean efficiency of 1.11.

Rank correlation coefficients between DMY measured in two blocks and various combinations of DMY and FMY measured in one or two blocks were all positive and high (Table 4). More accurate genotype rankings were achieved with two blocks relative to one block of

FMY. Rank correlations based on one block of DMY were significantly greater than two blocks of FMY for the conservation management trials but only marginally better than two blocks of FMY for the frequent-cutting management trials. The highest rank correlations were achieved with one block each of DMY and FMY, with both methods of adjustment of FMY to a DM basis of similar accuracy. The number of "correct selections" based on various combinations of DMY and FMY measured in one or two blocks ranged from 3.0 to 4.5 (Table 5) and followed a similar pattern to the corresponding rank correlation coefficients. The obvious limitation to both rank correlation coefficients and the number of "correct selections" as a measure of the efficiency of indirect selection is that differences between adjacent rankings may be very small in trials with elite germplasm. However, the

fundamental effects of various combinations of DMY and FMY measured in one or two blocks are highly applicable. Where land area or seed is limiting, selection for DMY based on one block of DMY is highly effective. Where both land, labor, and money are limiting, selection for DMY based on one block each of DMY and FMY offers a satisfactory alternative.

CONCLUSIONS

This study indicates that FMY can be successfully used as an indirect selection method of increasing DMY in perennial ryegrass sward plots with surface dry forage of similar ploidy, maturity category and management but at a considerable saving in resources where the requirement to sample and dry forage is eliminated. If the savings in resources from practicing indirect selection are re-allocated to

the evaluation of more plots, more genotypes rather than replicates should be included. Under such a scenario, indirect selection may be more effective than direct selection.

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